# THE REPRODUCTIVE BIOLOGY OF PROBOSCIDEA LOUISIANICA (MARTYNIACEAE)

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*Proboscidea louisianica* (Mill.) Thellung, found in temperate North America, is the most widely distributed representative of the Martyniaceae. It can be found growing in disturbed soils and waste places from West Virginia to Illinois and Minnesota and southward to Georgia and Mexico. The fruits with their vicious claw-like appendages give the plant its common name, Devil's Claw. Devil's Claw is an erect or prostrate freely branched summer annual which grows 3–8 dm tall. The entire plant is covered with viscid, glandular hairs whose secretions give the plant a fetid odor. The lavender, pink, or almost white flowers are strongly scented, borne in racemes of 8–20 flowers at the summit of the stems and branches, and have yellowish and purplish mottling inside the throat. The four stamens are didynamous.

Sexual reproduction in the Martyniaceae is somewhat unusual. The stigma is composed of two flat, sensitive lobes which rapidly close when touched (Figure 1). The lobes reopen after stimulation provided that no pollen has been placed on the stigmatic surface. However, when compatible pollen touches the stigmatic surface the lobes generally remain closed. The sensitive stigma of *Proboscidea louisianica* has been superficially investigated by Anderson (1922) and Thieret (1976) and both observed that the pollinators caused the closing of the stigma as they entered the flower but before contact with the anthers occurred. These observations suggested that the stigma functions to decrease the possibility of self-pollination. Additionally, Thieret suggested that self-polination was "fruitless" since his experiments indicated that *P. louisianica* was not self-compatible. The sensitive stigma and the compatibility among closely related annual species in the genus *Proboscidea* (Hevly, 1976) suggest that the reproductive biology of *P. louisianica* is unusual and worthy of further study. Therefore, a detailed study of *P. louisianica* was undertaken in order to elucidate its reproductive biology.

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## STUDY AREA

In June of 1976, five populations of *Proboscidea louisianica* were located on the north shore of Lake Texoma in Marshall County, Oklahoma, approximately two miles west of the University of Oklahoma Biological Station (Phillippi, 1977). It was unknown at the time that Thieret (1976) had observed plants in the same general area in 1973. In the past this region was covered by alternating tallgrass prairies and blackjack-postoak forests generally described as "The Cross Timbers". The soils are fine sandy loam soils of the Miller series formed during the Upper and Lower Cretaceous (Bennet, et al., 1912). At present, row crops and pastures dominate the landscape. The populations, occurring in overgrazed pastures and at the edge of fields, are in typical habitats for *P. louisianica.*

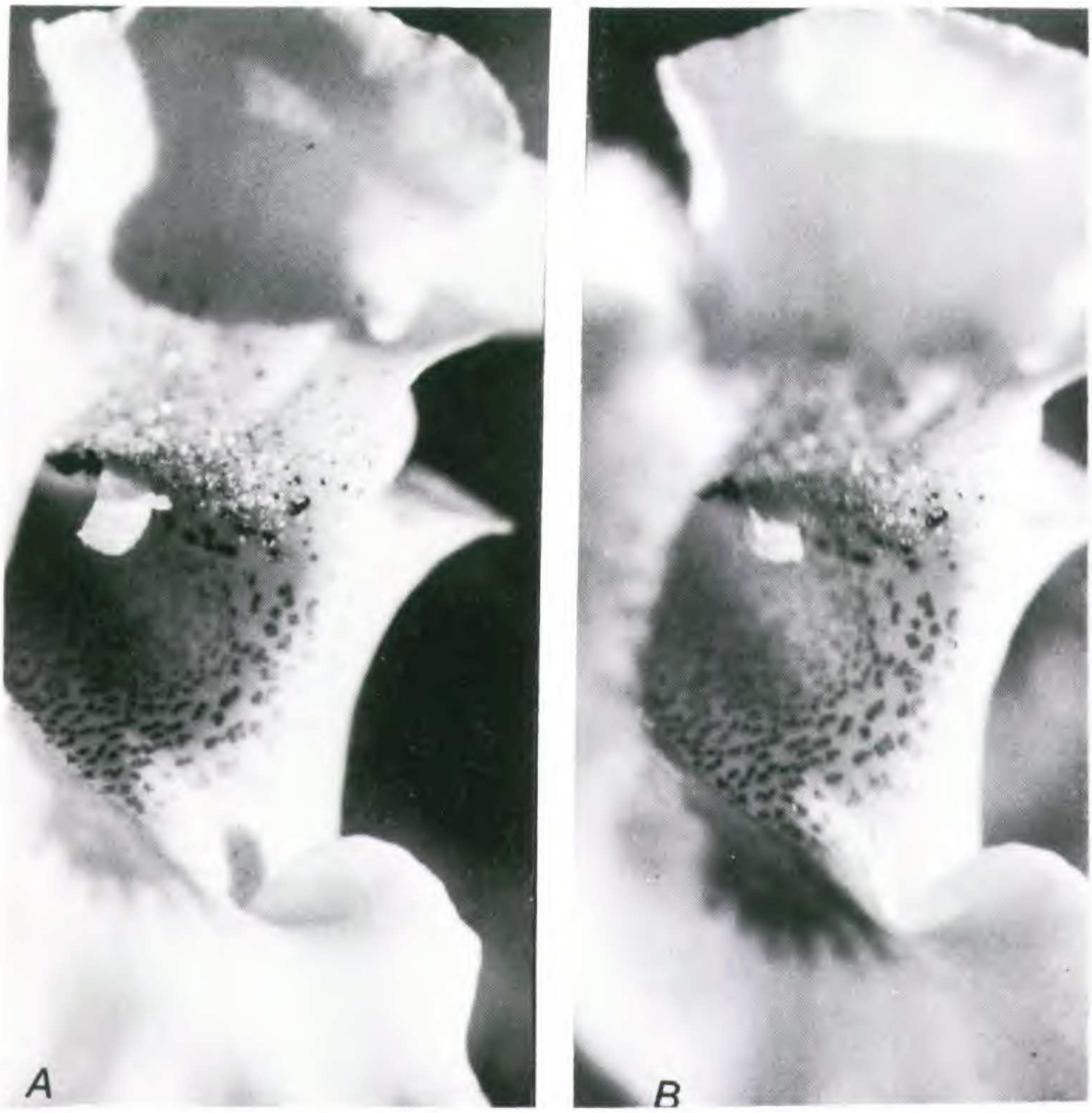


Figure 1. Flowers of *Proboscidea louisianica* with sensitive stigma visible at roof of the corolla tube. A. Open stigma lobes. B. Closed stigma lobes.

Collected insects were deposited in the Oklahoma State University Entomological Museum and the Snow Entomological Museum at the University of Kansas. Voucher specimens of *Proboscidea louisianica* have been placed in the Oklahoma State University Herbarium (OKLA). In each population, the phenology and fruit development of the plants, the insect visitors and their behavior, and the breeding system were examined.

## PHENOLOGY

The observations of Anderson (1922) and Thieret (1976) are combined with ours to describe the phenological patterns of *Proboscidea louisianica*. Flowering commences in late May or early June. After a bud reaches approximately 1.5 cm in length, development proceeds rapidly until the corolla reaches a length of 3–6 cm the day before opening. The time of opening is variable, usually occurring before noon, but flowers can be found opening at any hour of the day. This observation is at variance with Thieret's (1976) who reports that flowers generally open in the afternoon, usually about 6:00 p.m. On the first day of anthesis, the corolla is pale yellow or yellowish white (color 1A2 or 1A3 according to the 1961 classification of Kornerup & Wanscher). Dark yellow (4A8) guidelines extend from the center of the lower lobe into the tube. Dark magenta (13F6) spots mark the tube and the bases of the lobes. Shortly before the corolla drops off, some two to three days after opening, the inner lobes are often tinged with pink (11A2 to 13A3). As described by Thieret, the opening takes three to six hours as the upper and lateral lobes gradually open and become somewhat reflexed. When fully open the corolla throat is directed slightly downward, due to a bending of the basal portion of the corolla tube. In each raceme, only one or two flowers are open at a time.

The stamen filaments remain short until just prior to anthesis when they elongate into the throat of the corolla. The four anthers are paired one set behind the other in the corolla roof directly below and behind the stigma lobes (cf. Figure 2 of Thieret). The anthers dehisce longitudinally shortly after flower opening commences. The large, sticky pollen grains, with an average diameter of 80 $\mu$, are characterized by an exine that is irregularly thickened thus forming hexagonal surface patterns. The number of grains per anther was determined via direct observation and dilution-counting. Buds from

the five populations were collected, killed and fixed in Carnoy's solution and then stained in Snow's alcoholic-carmine. Buds 1–1.5 cm long from five different plants were selected from each population. One anther was excised from the bud and dissected in 20 ml of tapwater to release the grains. A 0.2 ml subsample of this mixture was pipetted while the water was rapidly agitated to assure uniform dispersion of the grains. The subsample was transferred to microscope slides and the grains were counted. Any grains left in the pipette were also counted. Three counts were made from each anther. The average number of grains per anther was 10,396 (9,200–13,000). The number of pollen grains per ovule was 850. This ratio is low when compared to those of other entomophilous species (Pohl, 1937) and may reflect the large size of the individual grains.

Pollen fertility was also examined. Five flowers from five different plants from each population were collected on the first day of anthesis. Pollen from each flower was scraped onto two slides. The grains on one slide were immediately stained with lactophenol: aniline blue (80ml:.05gm) and the first 200 grains observed were scored as either fertile or infertile. Darkly stained spherical pollen was scored as fertile, while pollen irregular in shape or faintly stained was scored as infertile. Percent fertility for all populations ranged from 92 to 96 with no significant difference between populations. Pollen on the second slide was placed in full sunlight for 48 hours, stained, and observed as before. No significant difference was detected between the fertility of two-day old pollen and that of freshly shed grains, which suggests that the pollen remains viable throughout anthesis.

To determine the time of pollen germination after deposition on the stigma, ten flowers were emasculated and bagged the night prior to opening. The next morning at 9:00 a.m. the flowers were hand-pollinated with pollen from another plant. Stigmas were collected at one-hour intervals following pollination, and fixed in a mixture of chloroform:ethanol:glacial acetic acid (6:3:1) and observed with a binocular microscope following staining with safranin O - aniline blue. The first pollen grains germinated within one hour of pollination.

Pollen tube growth was examined for both selfed and outcrossed plants. On the afternoon before flower opening, 60 flowers were bagged, half of which were emasculated. The following day at 6:00

p.m. 30 flowers were manually self-pollinated while the 30 remaining emasculated flowers were pollinated with pollen from other plants. At six-hour intervals throughout flowering, three selfed and three outcrossed plants were collected, killed and fixed in a 6:100 mixture of 37% commercial formalin to 70% ethanol (Chandler, 1931). Using the technique described by Ramming et al. (1973) the pollen tubes were stained with 0.005% water soluble aniline blue in a 0.15 *M* solution of $K_2HPO_4$ at pH 8.65 and the intact style and stigma squashed and observed by fluorescence microscopy. The pollen tube walls fluoresced a bright yellow-green. Pollen tubes reached the apex of the ovary in less than six hours with no observable difference between the growth of tubes in selfed and outcrossed plants.

The style is tubular and terminates in the two-lobed stigma. The lower lobe, with an average length of 2.5 mm, is substantially longer than the upper, which averages 2.1 mm long. Numerous viscid papillae cover the inner surfaces of both lobes. The stigma is exserted approximately 5 mm beyond the distal end of the anthers.

Stigma receptivity was examined. Thirty flowers were emasculated and bagged the night before opening. Beginning at 6:00 a.m. the following day, three flowers were hand-pollinated with pollen from another plant. Three stigmas were collected one hour after pollination, and fixed in the formalin:ethanol mixture. Thereafter stigmas were collected and fixed at six-hour intervals for 54 hours, or throughout anthesis. The stigmas were stained in a one percent solution of safranin-aniline blue (1:1) and examined for germinated pollen. Pollen tubes were observed on all stigmas, indicating that the stigma is receptive throughout anthesis.

At the base of the ovary is a dark green ring of cells that secretes nectar throughout anthesis. Ovules per ovary average 50 (range of 36-73, sample size = 25). Fruit development is rapid. Within one week after the corolla is shed, the fruit is several centimeters long with a green, fleshy pericarp. A unilocular, loculicidal capsule, the fruit is differentiated into a basal body 2–3 cm thick and 5–10 cm long and an arcuately-curved beak 15–20 cm long. Approximately two months after flowering, the exocarp sloughs away and the hard endocarp splits from the apex to the base forming the two horns or claws that give the fruit its name (Mayberry, 1947). This bizarre fruit facilitates seed dispersal as it is readily entangled in the legs of

herbivores, particularly cattle. Farmers, whose stock are tormented by the pain the fruit inflicts, describe the plant as a nuisance (Gardner, 1932).

## INSECT VISITORS AND POLLINATION

Observations of the flowers of *Proboscidea louisianica* reveal adaptations for insect pollination (Baker and Hurd, 1968; Faegri & van der Pijl, 1971). The flowers are of the "gullet-type" and are characterized by the sexual organs positioned at the roof of the corolla so that pollen is deposited on the dorsal parts of the pollinator, and by a prominent landing platform. In addition, flowers of *P. louisianica* exhibit typical adaptations for bee pollination as the flowers are zygomorphic and mechanically strong, possess well-hidden nectar, have nectar guides, and are odoriferous.

During the summer months of 1976, observations and collections were made of the insects visiting *Proboscidea louisianica* blossoms. The behavior of insects alighting on the corollas was recorded. The insects were then collected, pinned, and labeled. Insects collected were examined for *P. louisianica* pollen. Every part of the insect where pollen was visible under a binocular scope was scraped, and the pollen transferred to a microscope slide. The pollen grains were then stained with safranin-aniline blue and identified. No attempt was made to quantify the amount of *P. louisianica* pollen in relation to other grains present. Insect visitors bearing *P. louisianica* pollen are listed in Table 1 (cf. Appendix C in Phillippi, 1977). Other visitors observed and/or collected but without pollen include butterflies, syrphid flies, fruit flies, and thrips; there is no indication that any of these visitors play a role in the pollination of *Proboscidea*.

Because of their behavior, the frequency of visits, and the number of individuals observed, two bee species are considered the major pollinators of *Proboscidea louisianica* in south-central Oklahoma. The first bee, *Melissodes communis* Cresson, was found foraging on *Proboscidea* at the beginning of the summer. As circumscribed by Mitchell (1960), *Melissodes* is a relatively large genus (>100 spp.) of moderately robust hairy bees. Members of this genus are regarded as important pollinators of native plants and crops. Laberge (1956) reports that *M. communis* is highly polylectic and prefers flowers of the Fabaceae and Lamiaceae, particularly members of the genera

Table 1

**Insect visitors bearing *Proboscidea louisianica* pollen.**
Classification according to Mitchell (1960).

| | Number of Individuals Collected | Number of Individuals Bearing Pollen |
|---|---|---|
| Order Hymenoptera | | |
| Family Apidae | | |
| *Bombus p. pennsylvanicus* De G.[1] | 15 | 14 |
| Family Anthophoridae | | |
| *Melissodes communis* Cresson[2] | 25 | 21 |
| *Xenoglossa strenua* (Cresson)[2] | 9 | 7 |
| *Centris lanosa* Cresson[2] | 2 | 2 |
| *Anthophora walshii* Cresson[2] | 1 | 1 |
| *Melissodes* sp.[2] | 1 | 1 |
| Family Megachilidae | | |
| *Megachile montivaga* Cresson[3] | 2 | 2 |
| Family Halictidae | | |
| *Lasioglossum* (*Evylaeus*) sp.[2] | 2 | 2 |

[1]Identified by Dr. H. E. Milliron, New Martinsville, West Virginia.
[2]Identified by Dr. Charles D. Michener, University of Kansas.
[3]Identified by Dr. T. B. Mitchell, North Carolina State University.

*Melilotus* and *Medicago*. In addition, this species was collected from *P. louisianica* by Robertson (1928) and by Thieret (1976).

During the course of this study as many as five to ten *Melissodes communis* females were seen foraging simultaneously in the large populations of *Proboscidea louisianica*. No distinctive flight pattern was observed and flower visitation appeared random. These insects also showed no apparent preference for the younger, light yellow flowers or the older, pink flowers. When entering the flower, the bee lands on the lower lobe of the corolla and moves into the corolla tube. Occasionally it may turn upside down while inside the corolla so that pollen is deposited both ventrally and dorsally.

Only females, 12–16 mm long, were captured and of the 25 individuals collected, pollen of *Proboscidea louisianica* was found on the head, thorax, abdomen, and scopae of twenty-one. Pollen is a rich source of food, especially protein, and is used in nourishing the larvae. The bees were also observed utilizing the nectar, probably for individual maintenance (Faegri & vand der Pijl, 1971).

*Melissodes communis* was observed and collected primarily in June, July and early August. Thereafter, these bees were only rarely seen. According to Laberge (1956) *M. communis* is most abundant from the end of June through August, but can be collected from March to September. The abrupt decrease of *M. communis* cannot be explained adequately, as *Proboscidea* was still in full bloom and there was no substantial increase in flowering of other plants that might have attracted the bees. *Melissodes communis* is thus believed to be a major pollinator of *P. louisianica*. The geograhic extent of this specific relationship awaits further collections from other populations of *P. louisianica* throughout its range.

In June, July and early August, *Mellisodes communis* was the only regular visitor to *Proboscidea*. In early August the number of *M. communis* visits decreased; at the same time, workers of *Bombus pennsylvanicus pennsylvanicus* De G. began visiting *P. louisianica*. Although visiting *Sloanum rostratum*, *Monarda punctata*, and *Helianthus annuus* which occurred among the populations of *P. louisianica*, this large bumblebee had not previously been observed landing on *Proboscidea*. It became the major pollinator throughout the remainder of *Proboscidea's* flowering season, which ended in early September. *Bombus p. pennsylvanicus* is distributed throughout northern Mexico, the United States, and southern Canada.

The bumblebee approaches the flower, lands on the lower lobe, and moves as far into the corolla as it is able. Pollen of *Proboscidea louisianica* was identified on 14 of the 15 individuals, being collected from the dorsal portions of the head and thorax as well as in the scopae. The bumblebees were also observed utilizing nectar. *Bombus pennsylvanicus* individuals were observed visiting *Solanum rostratum* and *Monarda punctata* as well as *P. louisianica*. This is to be expected since a colony is active throughout the growing season because of the overlapping generations of adults; the bees exploit a wide variety of plant species as they become seasonally available (Heinrich, 1976).

*Solanum rostratum* and *Monarda punctata* came into bloom later than *Proboscidea louisianica;* perhaps it was these species that at first attracted *Bombus pennsylvanicus* into the populations of Devil's Claw, during which time the bumblebee began "minoring" (Oster and Heinrich, 1976) on *P. louisianica,* then eventually "majoring" on it. The first pollinator's decline is unexplained at this point. No acts of aggression were observed between *Mellisodes communis* and *B. pennsylvanicus* and according to Heinrich (1976) it is "unlikely that [bumblebee] colonies can seize, hold or defend territories . . . they do not give any sign of intolerance of [other species] while foraging under natural conditions."

Both putative pollinators remove almost all of the pollen from the anthers of each flower. Observations of 25 newly opened flowers on two occasions (n = 50) revealed that all of the flowers were visited at least once before noon of the first day of anthesis. Pollen grains were packed in the scopae and on the head and thorax of *Bombus* and the head, thorax, and abdomen of *Melissodes.* Kraai (1962) suggests that pollen packed in the scopae does not play a role in pollination as viability is quickly diminished. The entrance of both bees into the corolla invariably stimulated the sensitive stigma to close so that its receptive surfaces were no longer exposed. The lower stigma lobe hangs down into the mouth of the corolla and comes into contact with the head, thorax, or abdomen of the entering visitor and at that time pollen from another plant is deposited on the stigma. When the pollen dusted bee exits the corolla there is little chance that self-pollination will occur, since the lobes of the stigma are closed. These observations are at variance with Thieret's (1976), who reported infrequent insect visits and the lack of pollen deposition on the stigmas of many flowers. This difference in observation can perhaps be attributed to our more intensive study and to the population dynamics of *Melissodes* and *Bombus.*

## THE SENSITIVE STIGMA

The sensitive stigma is not unique to the Martyniaceae but has been described from species in the Bignoniaceae (Burck, 1902; Newcombe, 1922), Lentibulariaceae (Hildebrand, 1869), Acanthaceae (Morren, 1839; Trelease, 1882) and the Scrophulariaceae (Henderson, 1841; Burck, 1902). In most cases, an insect pollinator

serves as the stimulating agent; however, Elrod (1904) observed hummingbirds fulfilling this role in *Campsis radicans* (L.) Seeman. The external morphologies of the stigmas are generally similar, and consist of two obovate to oblanceolate lobes which diverge at varying angles from 90° to nearly 360°, prior to stimulation and closing. In one genus of the Acanthaceae, *Strobilanthes*, the sensitive stigma consists of a slender style that tapers at its apex to form the stigma. In this case, the stigma and style quickly straighten and recurve upon stimulation so as to press the stigma closely against the lower lobe (Trelease, 1882).

Another common attribute of these sensitive bilobed stigmas is that the lobes reopen after stimulation, provided that no pollen has been deposited on the stigmatic surface (Newcombe, 1922). However, when compatible pollen touches the stigmatic surface the lobes generally remain closed. The sensitive stigma has been generally considered to function to decrease the possibility of self-pollination. However, Burck (1902) found that the sensitive stigma of *Torenia fournieri* (Scrophulariaceae) functioned to increase the possibility of self-pollination. Burck (1902), Lloyd (1911), and Brown (1913) investigated the response mechanism and concluded that water withdrawal from the lobes was responsible for the stigmatic closure. Newcombe (1922) confirmed their findings and, in addition, gathered evidence which suggested that an enzyme or other chemical substance in the pollen maintained closure.

Heckel first described the sensitive stigma of *Proboscidea louisianica* in 1874. Rain or a water droplet would close the stigma momentarily, which reopened in five to ten minutes. Sand dusted over the lobes, as well as blowing on the lobes, would also cause temporary closure. The stigma is sensitive to very slight stimulations and can readily be closed by pulling a human hair across the lobes. Observations concerning fatigue of the stigma agree with those of Brown (1913) and Thieret (1976). The first stimulation of the stigma at the beginning of anthesis requires five to ten minutes to reopen. On the 5th, 6th, or 7th stimulation, reopening generally requires 25–45 minutes, stimulation after that requires up to two hours.

Observations during the present study suggest that the stigma of *Proboscidea louisianica* functions primarily to decrease the possibility of self-pollination. The stigma may also serve to protect the germinating pollen physically.

## THE BREEDING SYSTEM

In order to determine the nature of the breeding system in *Proboscidea louisianica,* different modes of reproduction were tested using standard techniques. All plants in each population were numbered. Fifty flowers at approximately the same stage of development were randomly selected in each treatment. Fruit set was checked one month later. Modes of reproduction tested and the methods employed were:

**Controls:** In order to estimate the percent fruit set under natural conditions, flowers were marked with a piece of fluorescent ribbon, but otherwise undisturbed.

**Anemophily:** Flowers were emasculated before pollen dehiscence, nylon stocking securely tied around the blossom and adjusted so that the stigma was exposed to the wind. The nylon stocking served to exclude insects but not air-borne pollen.

**Agamospermy:** Flowers were emasculated while still in the bud and bagged to prevent pollen from reaching the stigma.

**Intrapopulational Xenogamy:** Buds were emasculated and bagged. At early anthesis stigmas were hand pollinated with the pollen from another plant in the same population and then re-bagged.

**Interpopulational Xenogamy:** Buds in population A were emasculated and bagged. While the bagged flowers were in early anthesis flowers from population C were collected, placed in separate four-dram vials, and the pollen was transferred to the stigmas of the bagged flowers in population A. Flowers were then re-bagged. Reciprocal crosses were made.

**Natural Autogamy:** Flowers were bagged while still in bud to test for natural self-fertilization.

**Artificial Autogamy:** Flowers were bagged while in the bud. During early anthesis, stigmas were manually self-pollinated and re-bagged.

The results of these crosses are summarized in Table 2. As expected, wind pollination is not part of the breeding system of *Proboscidea louisianica* as the flowers lack the structural modifica-

Table 2

**Percent fruit set under experimental conditions.**
No significant differences among populations at 5% level, population results pooled.

| Mode of reproduction tested for | Number of flowers | Percent fruit set |
|---|---|---|
| Controls | 42 | 52 |
| Anemophily | 46 | 0 |
| Agamospermy | 75 | 1 |
| Intrapopulational Xenogamy | 47 | 83 |
| Interpopulational Xenogamy | 49 | 78 |
| Natural Autogamy | 48 | 4 |
| Artificial Autogamy | 47 | 57 |

tions generally associated with anemophily (Faegri & van der Pijl, 1971). *Proboscidea* also does not appear to be agamospermous; the one fruit occurring in population A was most likely due to an error in technique. Twenty-five additional flowers were tested in that population, none of which set fruit.

Intrapopulational and interpopulational crosses were equally successful. There was no significant difference between these two modes of reproduction ($p > .5$)*. However, a significant difference was observed between these crosses and the control percent fruit set ($p < .02$), but this was most likely due to the extensive predation of control flowers by lepidopteran larvae that foraged on *P. louisianica* throughout the summer. Bagged flowers utilized in the crossing experiments were protected somewhat from this predation.

Natural autogamy, in the absence of biotic pollinators, does not play a significant role in the reproduction of *P. louisianica* as indicated by the 4% fruit set. On the other hand, the taxon is self-compatible (57%) when manually self-pollinated. The previously

*All values of p refer to the t-test.

described spatial relationship of the essential organs and the exclusion of biotic pollinators are responsible for the lack of natural selfing. In addition, there seems to be an internal isolating mechanism partially preventing self-fertilization. There was a significant difference ($p < .05$) in fruit set between artificially selfed and outcrossed plants. As previously mentioned, a comparison of pollen tube growth between selfed and outcrossed plants did not reveal any differences. There was no distinguishable difference in the autogamous fruits either during development or in the number of seeds set per fruit ($p > .5$) (Table 3). Furthermore, there was no significant difference ($p > .5$) in the percent germination of the seeds from selfed or outcrossed fruits (Table 4). It is suggested that the barrier is prezygotic, perhaps a failure of the pollen tubes to penetrate the embryo sac consistently.

Cytological studies of *Proboscidea* began with investigations by Anderson (1922) who described the development of the flower, sporogenesis, and gametogenesis. Chromosome counts of $2n = 30$ were made by Martini (1939) and Perry (1924) which are confirmed. Buds were collected, killed and fixed in chloroform: 95% ethanol: glacial acetic acid (6:3:1), bulk stained in Snow's alcoholic-carmine, and dissected anthers squashed in Hoyer's medium. Meiotic con-

Table 3

**Seeds per fruit in selfed versus outcrossed fruits from populations A and C.**

| | Population | | |
|---|---|---|---|
| Selfed | A | C | A & C |
| Number of fruit | 4 | 10 | 14 |
| Number of seeds | 249 | 427 | 676 |
| Average number of seeds/fruit | 62.25 | 42.7 | 46.8 |
| Outcrossed | | | |
| Number of fruit | 5 | 15 | 20 |
| Number of seeds | 266 | 636 | 902 |
| Average number of seeds/fruit | 53.25 | 42.4 | 45.0 |

Table 4

**Percent germination of selfed versus crossed seeds from populations A and C[1].**

| | Population | | |
|---|---|---|---|
| Selfed | A | C | A & C |
| Number of seeds | 249 | 427 | 676 |
| % germination | 57 | 6 | 25 |
| Crossed | | | |
| Number of seeds | 266 | 636 | 902 |
| % germination | 40 | 8 | 18 |

[1]Normal fruit development requires approximately eight weeks. Germination of seeds from eight week old fruits or older is 75%. Fruits of populations A and C were collected early (six and three weeks respectively) because of extensive rodent and insect predation.

figurations of 70 microsporocytes from 26 plants from all 5 populations were analyzed. Pairing and disjunction of the chromosomes is quite regular with 15 bivalents at Metaphase I. Chiasmata number and position is fairly constant with 52% of the bivalents characterized by one terminal chiasma, 35% by two terminal, 10% by one interstitial and one terminal, and 3% by one interstitial chiasma. Fifteen dyads were observed consistently in Anaphase I. Cytokinesis is post-meiotic.

## SUMMARY

A detailed study of five populations of *Proboscidea louisianica* in south-central Oklahoma was undertaken to determine its breeding system, phenological patterns, and principal pollinators. Major findings are that:

1. *Proboscidea louisianica* is an outcrosser capable of autogamy. The sensitive bilobed stigma is the mechanism that facilitates xenogamy. A pre-zygotic barrier to self-fertilization is hypothesized to exist.

2. Of the eight insect taxa utilizing pollen of *P. louisianica* two, *Melissodes communis* and *Bombus pennsylvanicus pennsylvanicus,* are considered major pollinators.

Possessing attributes favoring both genecologic flexibility and fitness, *Proboscidea louisianica* is adapted for dispersal and occurrence in disturbed habitats. This is a common characteristic of autogamous plants, as Stebbins (1958) demonstrated. It is conceivable that before rangeland was fenced, there was considerable long-distance dispersal of the Devil's Claw fruits by large herbivores. At present, the fruits of *P. louisianica* are thought to be dispersed by certain agricultural practices (Gardner, 1932). Self-compatibility makes it possible for a single plant to reproduce and start a population.

Perpetual self-fertilization does have its disadvantages. Continued inbreeding tends to reduce heterozygosity, recombination, variability, and therefore the evolutionary potential of a species. On the other hand, outcrossing promotes genetic recombination and thus genetic diversity which is likely to lead to ecologic diversity. Therefore, a plant such as *Proboscidea louisianica* whose reproductive mechanisms encompass both cross- and self-fertilization is likely to be successful in invading new habitats.

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